PRINCIPLES OF PLANT TAXONOMY. IX.*

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In the eighth paper† of the present series, a general synopsis of the Thallophyta was given, together with a diagramatic "tree" of relationships of the orders recognized. Since the fungi are of special importance and are thus often studied independently of other groups and since the true fungi evolved a distinctive type of plant body and cell constitution, the following analysis is presented as a partial explanation of the arrangement of the groups in the synopsis. Special attention has been given to the development of correct interpretations of life histories in the light of special studies on the problem of sex in plants in general as well as comparative studies of life cycles.

THE FOUR GENERAL TYPES OF FUNGI.

If we use the term Fungi to include all Thallophytes without chlorophyll, then these plants fall into at least four distinctive, fundamental groups or great phyla. The various kinds of bacteria, including the slime bacteria (Myxobacteriales), show a very profound segregation from the remaining groups and are closely associated with the blue-green algæ in the Schizophyta.

The saprophytic slime-molds constitute a very distinct phylum of their own, whose nearest relatives are probably to be found among the Rhizopoda of the animal kingdom on the one hand and among the Archemycetæ on the other, especially the Plasmodiophorales. But they are, nevertheless, so widely divergent from either of these groups that they are best considered as a distinct phylum which has evolved along its own lines from a very primitive starting point.

The two classes, Archemycetæ and Monoblepharideæ, show a decided correspondence to various groups of the great mother phylum, the Gonidiophyta consisting mostly of flagellate green algæ. They appear to be members of this group which have lost their chlorophyll. These two classes differ in various respects from the true fungi (Mycophyta). The Archemycetæ

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have nothing that can properly be called a mycelium. They range from forms apparently without sex, but which may nevertheless have this potentiality, to forms with well developed sexual conditions. The conjugations of the sexual forms are, however, of the more primitive and normal types of sexual fusions and not the highly specialized condition of the Mycophyta. The Monoblepharideæ are plainly a direct offshoot from the Siphonocladales of the Gonidiophyta and have the sexual processes which are typical for the higher green algæ. A *Monoblepharis* is simply a green alga that has lost its chlorophyll, in the same general sense that *Cuscuta* and *Monotropa* are Angiospermæ that have lost their chlorophyll.

The remaining chlorophylless thallophytes are the true fungi and make up the phylum Mycophyta. This phylum is characterized by its peculiar vegetative body, the mycelium, and by a specialized sexual process, the conjugation nearly always taking place between the walled sexual cells or branches. Such a process occurs only in one other group, the higher Zygophyta, with which the fungi show no close correspondence otherwise. The Mycophyta are also to be derived from the great mother group of green algæ, the Gonidiophyta. The correspondence in the original life cycle and filamentous body is very great. The normal green alga has a simple haploid sexual cycle, the only diploid nucleus being in the zygote. The true fungi have exactly this cycle at the lower levels and the higher forms have evolved a direct modification of it. There is no correspondence with any other of the higher thallophyte phyla. Neither the red or brown algæ nor the Charophyta whose life histories have been worked out have such a life cycle. The supposed correspondence of some fungi with the red algæ is entirely superficial. Fungi could not be derived from red algæ without a complete recreation of almost the entire ontogeny. Whether one derives the Mycophyta by a separate line from the green algæ or through a series of Archemycetæ is of no fundamental phyletic importance since in either case the primary derivation must be from the green-algal complex.

The Mycophyta fall immediately into two very distinct subphyla, Phycomycetæ and Mycomycetæ. The first group is cenocytic, the second has a mycelium of normal cells although cenocytic developments may be present. Now we can derive these two groups independently from the green algæ, the first

from the cenocytic Siphonocladeæ, the second from the Conferveæ. Or what is just as reasonable from the present evidence, we can say that they had a common origin as fungi, and then after being segrated from the algal line as chlorophylless plants they divided into two phyletic series in the same way as the green algæ, divided into cenocytic groups and groups which have their filaments made up of normal cells.

At the transition from green plants to typical Mycophyta the fungi were probably still isogamous or nearly so and then evolved to various degrees of heterogamy. The progress of the sexual condition was influenced by several peculiar developments which led away from the typical course of sexual evolution as it appeared in the main line of plants from the green algæ to the seed plants.

In some of the lower groups of fungi zoospores are characteristic cells of the life cycle in others and in all of the higher fungi no zoospores are in evidence. Here again we can have the choice of two alternatives in speculating on phyletic origins. For just as some green algæ in a water habitat have zoospores and some have not and the same in respect to the two great phyla of Phaeophyta and Rhodophyta, so our ancestral Mycophyta may all have had zoospores and then mutated into nonmotile forms after or at the time they took up an aerial life; or they may have developed the two types of motile and nonmotile spores and gametes before they passed from the water, if it is true that they became fungi before taking up an aerial life. It is perfectly evident that the absence of zoospores in a group is no criterion for assuming that such absence is the result of aerial conditions.

In general, the lower fungi have a loose undifferentiated condition of the mycelium while as one ascends the scale a more and more complex body is evolved, until the truly marvelous is reached in the higher Pezizales and Phallales. This complex interacting system has thus taken the same general course and direction as that which has evolved in the solid aggregates of the higher, vascular plants. But the development of complex tissue systems and organs in the fungi appears much more remarkable because the unitary interaction is accomplished through a branching system of filaments rather than in the closely packed contiguous cells of a solid tissue. Along with the development of a complex interaction and correlation system goes the development of diverse chemicals, colors and

substances, duplicating in a remarkable manner the same evolutionary movements in evidence in the higher vascular plants.

The phylogenetic movement in the rusts is in evidence not so much in the evolution of the plant body as in the complexity of the spore forms. The Teliosporæ, therefore, make up a phyletic line which advanced in a different direction from the typical Basidiomycetæ.

There are several difficult problems which come in with a consideration of the Laboulbenieæ. These plants must have segregated as a distinct phyletic line from the primitive Ascomycetæ almost from the beginning and have therefore both a peculiar fungous body (which can hardly be called a mycelium) and some very distinctive reproductive characteristics. Apparently the life cycle is the typical simple haploid sexual cycle and the slight superficial resemblances to certain features of the red algæ must be regarded like other accidental mimicries, which indicate neither phylogenetic relationships nor even a common causal basis. The development of conidia in the male reproductive branches of some Laboulbenieæ as well as in some discomycetous lichens is to be explained by the assumption of the presence of hereditary factors which give a proper functional gradient in the antheridial branch so as to throw conidium-producing heredity into activity at this point. This process does not interfere with the primary sexualization of the cells involved and thus these cells act as normal male cells in reaction with the trichogyne of the ovary. In all such cases attention must be fixed on the complex of hereditary potentialties, which are thrown into activity or latency through the development of the proper physiological states in the cells involved. The plant is not built up of "bricks and boards" but by a functional process which is induced through the interaction of the hereditary potentialities, the progress of the physiological and ontological gradients in the given parts, and the influence of the immediate environment. The old morphological speculations are largely beside the mark. When for example we cause stigmas to grow out of the tips of stamens or microsporangia to develop in the walls of an ovulary, the result does not mean that these structures were ever so associated phylogenetically but simply that we have disturbed the normal functional gradients and the normal physiological states of the cells by changing the usual environment. So also in the

evolution of a series of plants, new potentialities may appear which will produce changed functional gradients and changed physiological states in the cells at the given ontogenetic point; and thus new and somewhat different expressions from the earlier ones appear.

The origin of endogenous spermatia must be regarded as a secondary development unless it is a hold-over from a more primitive condition which is not likely. It is far more reasonable to assume a secondary conidium-like development on the order of the peculiar conidia of Thielavia where they are developed in a sheath. Whatever one may conclude as to the origin and final relationships of the Laboulbenieæ, it is far better to set them aside as a distinct class from the other Ascomycetæ. This disposal will show the very decided way in which they have digressed from the other Mycomycetæ in general and from the Ascomycetæ in particular.

THE EVOLUTION OF THE FUNGUS LIFE CYCLE.

As stated above the life cycle of the typical fungi is the simple haploid sexual cycle or some direct modification of this. (See Figs. 1 and 2.) There is no alternation of generations, the only diploid cell being the zygote. (See Fig. 3.) Some phases of the life cycle of the fungi have been discussed previously by the writer which may be considered in this connection.* The incipient ascus and incipient basidium are homologous structures and really represent the zygote in general. The basidium is the more specialized structure. This does not mean, however, that the basidium is a transformed ascus, or that it is to be derived from an ascus. Both structures have probably been derived from a simpler condition which would not properly be called either an ascus or a basidium. The septation of the basidium has taken place independently in several lines of Teliosporæ and Basidiomycetæ. Such parallel developments occur very commonly in diverse groups of higher plants and are not to be interpreted as indicating direct relationships unless the other morphological and physiological characteristics are in agreement.

The lower groups of the various series are mostly hermaphroditic (homothallic) and this condition may continue to a

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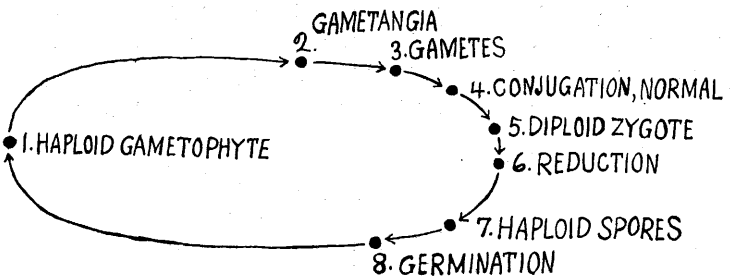

FIG. I.

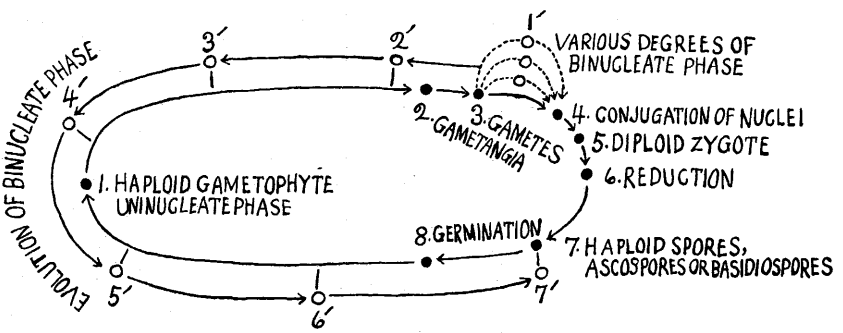

FIG. II.

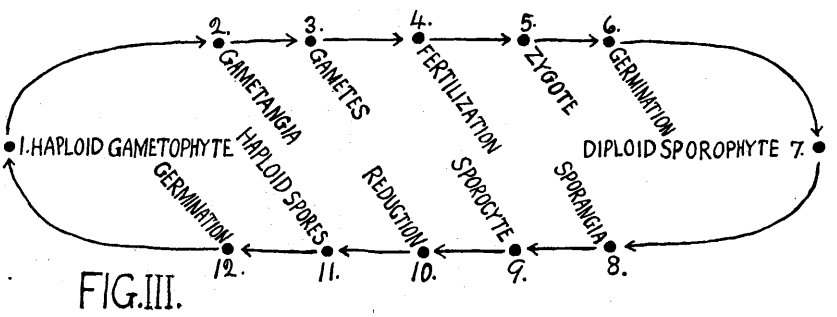

FIG. III.

EXPLANATION OF FIGS. 1, 2 AND 3.

FIG. 1. The normal simple haploid sexual life cycle.

FIG. 2. Diagrammatic representation of the evolution of a conjugate phase by modification of the simple haploid sexual life cycle of the lower fungi.

FIG. 3. The typical antithetic alternation of generations cycle which shows that there is no real alternation of generations of any kind in the fungi.

very high stage or even to the highest, as is also the case with bisporangiate flowers in the Anthophyta. As the series evolve, they usually develop species with unisexual individuals, female (+) and male (−), or heterothallism. The peculiar evolution of the binucleate phase in the highest species makes heterothallism, in the ordinary sense, impossible, since the plus (+) and minus (−) conditions are manifest only in the conjugate nuclei, and the synaptic chromosome mates. In the extreme species the entire mycelium is binucleate and the plus (+) and minus (−) states are in the inside of every cell. In addition to the remarkable development of the incomplete primary sexual states there also appears to be an evolution, in some groups, of decided physiological compatibilities and incompatibilities between various chromosome combinations, so that the ability to conjugate may involve more than the mere fact of plus and minus strains. These phenomena are comparable to the numerous physiological strains which involve the resistance and susceptibility of host plants, as in certain smuts. There have been various fantastic interpretations of the phenomena, but it is evident that the diverse types of mycelia produced with consequent incompatibilities of sex reaction do not mean that the Basidiomycetæ have an indefinite number of "sexes" but rather that the same kind of physiological conditions arise, because of the presence of specific chromosomes in the given nuclei, as those which interfere with the conjugation of sperms and eggs of diverse species of plants and animals.

The life cycle of an ordinary green alga or of a lower fungus is shown in figure 1. This, as stated, is the simple haploid sexual cycle. *Eremascus fertilis* has such a cycle except that the four haploid nuclei resulting from reduction are increased to eight by the addition of a vegetative division, giving eight ascospores instead of four which is the more common number following a reduction division. In *Coleochaete* the divisions are also multiplied after reduction. *Eremascus albus* has the same cycle and apparently the Phycomycetæ in general also. In figure 2 this simple haploid sexual cycle is indicated by the stages marked 1-2-3-4-5-6-7-8. When one passes from the Phycomycetæ to the lower Ascomycetæ, a very remarkable condition becomes evident through the intercalation of a binucleate phase between the cytoplasmic conjugation of the walled gametes and the final conjugation of the male and female nuclei to form the zygote. The first evidence of such a con-

dition evolving is the long delay in the fusion of the paired nuclei after they lie together in the fusion cytoplasm. This condition is present in some Zygomycetæ and in *Endogone lactiflua* where nuclear fusion is apparently not accomplished until the time of germination of the zygote (See Fig. 2=7-8-1-2-3-1′-4-5-6). In *Endogone pisiformis* fusion is said to occur shortly after copulation of the sexual branches. (See Figs. 1 or 2=7-8-1′-2-3-4-5-6). Some Oomycetæ also appear to have delayed nuclear fusion.

Now this condition of a partial attractive and interactive property of gametes, which for the time being falls short of complete nuclear fusion, the writer has called the incomplete or partial primary sexual state. Such states develop in the gametes of certain species of *Oedogonium* and *Bulbochaete*, where, although the original sperms (androspores) are attracted, no fusion of cells takes place for the time being but the androspores develop into dwarf males.

To gain a correct understanding of the peculiarities of sexual expression of the higher fungi, it is necessary also to take into account the various sexual states which may be present and their influence on the behaviour of the protoplast. The sexual states evident are: (1) Neutral state; (2) male and female secondary sexual states, which influence hereditary expression but do not induce attraction and fusion; (3) incomplete male and female primary sexual states, which induce attraction and in the fungi copulation of the cells involved but not a fusion of the nuclei, the nuclei nevertheless exerting an influence on each other so that they act harmoneously; and (5) complete male and female primary sexual states, which induce not only attraction but complete fusion of the nuclei, resulting in the organization of a unitary diploid nucleus; and at a later stage through the individual sexualization of the chromosomes, during the reduction division, giving rise to pairing and temporary fusion of the synaptic chromosome mates.

Now as stated above the delay of the fusion process in some of the lower fungi indicates a delay in the complete primary sexualization of the fusion nuclei. This delay turus out to be the initial stage of a remarkable orthogenetic evoln-tionary series; for the next step is the intercalation of vegetative divisions in the pair of conjugate nuclei, giving rise to the conjugate vegetative phase of the life cycle. In the lowest stages of this evolutionary movement, only a few divisions

take place, giving rise to small binucleate ascogenous hyphæ, on which the incipient asci are developed, in which, with complete primary sexualization of the conjugate nuclei, the diploid zygote nucleus is produced. This condition is present in such low Ascomycetæ as *Pyronema*, *Phyllactinia corylea*, etc., where the sexual cells or organs are slightly dimorphic. This dimorphism is due to a slight evolution of secondary sexual states which come to expression in the cells involved. After the copulation of the conjugate cells, the pair of conjugate nuclei undergo conjugate divisions in the small ascogenous hyphæ. The conjugate phase is soon ended by the formation of the hook-shaped processes at the tips of the binucleate hyphæ. This hook-shaped process must be regarded as a result of secondary sexualization of the cell concerned. The influence surrounding the male conjugate nucleus having its effect, at this stage, on the surrounding protoplasm while the cytoplasmic field surrounding the female conjugate nucleus is influenced in a different way. This differential secondary sexual condition is more marked in the higher Basidiomycetæ and is responsible for the development of clamp connections which are to be compared to the dimorphic development of the pair of gametangia in such algæ as *Vaucheria sessilis* and more especially with the end to end conjugation apparatus developed in some species of *Spirogyra*. Such similarity of morphological expression is to be looked upon as parallelism just as there are numerous parallel developments from isogamy to heterogamy or the evolution of secondary sexual states beyond the gametangia.

Not only is there an orthogenetic evolutionary advancement in the conjugate phase but there soon appears a characteristic movement, into earlier stages of the ontogeny, of the initiation of the incomplete primary sexual states or the time of determination of the conjugate phase. Thus the original conjugating cells or gametangia disappear since the secondary sexual states which arise in the new vegetative conjugating cells are apparently not intense enough in many cases to produce such dimorphism although in the higher Basidomycetæ some dimorphism does appear in connection with the development of clamp connections.

In some of the higher Ascomycetæ, as in *Humaria rutilans* and *Helvella*, the time of development of the incomplete primary sexualization is shifted backward in the ontogeny so that conjugation of the two cells takes place in the hyphæ of the hypo-

thecium. The life cycle is then approximately represented by Fig. 2=7-8-1-3′-2′-1′-4-5-6. These plants may, of course, have been in an isogamous condition when the conjugate phase began to evolve and then never got beyond this condition.

In the basidiomycetous series the development of the conjugate phase has gone farther as one would expect, from their more advanced condition in general structure and function. In the common rust, *Puccinia graminis* the uninucleate phase is developed on the barberry and ends with the aeciospores. The nature of the sexual conditions is not yet entirely cleared up but the plus and minus sexualization seems to be accomplished in contiguous cells in the base of the aecium. The nature of the pycnium is obscure, but it is not probable that it ever had anything to do directly with an antheridium phylogenetically even though it might be shown to develop male states at present. Much investigation remains to be done on the rusts before their variously complicated life cycles can be properly homologized. There are probably both homothallic and heterothallic primary mycelia present. In the smuts there is sometimes a short uninucleate phase, the binucleate phase being originated through the conjugation of sprout cells which are vegetative descendants of the basidiospores. The life cycle would then be according to the scheme of Fig 2=7-8-6′-5′-4′-3′-2′-1′-4-5-6. In the Tilletiales as in *Tilletia tritici*, the movement has proceeded further and the incomplete primary sexualization takes place in the basidiospores which then promptly conjugate and thus initiate the binucleate phase (Fig. 2=7-7′-6′-5′-4′-3′-2′-1′-4-5-6). In *Ustilago nuda* the movement has gone one step further. The four cells of the basidium (promycelium) which really represent four reduction spores or undifferentiated basidiospores develop the incomplete primary sexual states and thus initiate the binucleate phase. Now the fact that these smuts have evolved the binucleate phase to the limit is not to be taken as a criterion for placing them at the top of the taxonomic series of basidiomycetous forms. They are at the top of the conjugate series just as cycads have advanced to the extreme, diecious condition while sunflowers still have bisporangiate flowers. This condition does not place sunflowers below cycads. The general level of a species or group must be judged by the combined levels of all the evolutionary movements present.

Apparently some of the Basidiomycetæ still have a short uninucleate phase at the beginning of their life cycle. Their

cycle will then be represented by Fig. 2=7-8-6′ or 5′-4′-3′-2′-1′-4-5-6. Such a condition is apparently present in *Collybia conigena*, *Coprinus fimetarius*, etc. In species of this type cenocytic divisions may sometimes be present at first but these cenocytic developments have no direct bearing on the evolution of the conjugate phase.

In *Corticium* and apparently in many Gasteromycetæ the mature basidiospores are binucleate and subsequent divisions are of the conjugate type. The entire mycelium is therefore, binucleate. In *Secotium* according to Cunningham, each basidiospore receives one of the four reduction nuclei and the spores become binucleate promptly by division. On germination a germ tube is produced which branches abundantly, forming a septate mycelium and all the cells are binucleate. Thus the incomplete plus and minus primary sexualization is accomplished at the very beginning in two vegetative sister nuclei and conjugation of walled cells, or copulation, is entirely eliminated. There is also no more possibility for the development of a heterothallic mycellium. The evolutionary movement of incomplete primary sexualization has proceeded to the very limit. In *Secotium* the life cycle is thus as in Fig. 2= 7-7′-6′-5′-4′-3′-2′-1′-4-5-6. Apparently the life cycles of *Lycoperdon excipuliforme* and of *Cyathus*, as reported, are quite similar.

The condition in *Secotium* is only the extreme vestige of the homothallic condition. In some Basidiomycetæ heterothallic conditions are present. The sexual states are determined in the initial nucleus of the basidiospores through functional states which to some extent may coincide with the presence of differential chromosomes distributed in the reduction division. In addition there may be combinations of physiological races or physiological states depending on individual chromosomes which may give compatible and incompatible reactions in connection with the sexual states developed, as discussed above. Referring only to the development of sexual states in relation to differential chromosomes, the conjugation of basidiospores, when such takes place, might be between homothallic pairs (homothallic condition) or between heterothallic pairs (heterothallic condition). If copulation of walled cells is eliminated, the two nuclei which come to be included in the basidiospore may also be homomorphic (homothallic condition—*Secotium*) or they might possibly also be heteromorphic and thus the vestige of a heterothallic condition.

The development of numerous reaction systems is not necessarily ascribed to a complexity of hereditary units shifted in the reduction division. There may be physiological differentiation giving peculiar sexual reactions and degrees of sexual compatibility and incompatibility, just as we have bacteria with intensified or attentuated virulence, depending apparently on the environmental conditions in which the organism is growing. Or as the two dichotomous buds of a Lycopodium, although having exactly the same hereditary constitution, react differently, the one growing against the force of gravity and the other at right angles to it. Or as in the sexual incompatibility developed in many flowering plants where the differentation processes going on in certain types of hereditary constitutions result in complete self-sterility, while compatibility is shown with another individual.

The clamp connections are to be interpreted as due to secondary sexual states arising in the respective fields of influence of the plus (+) and minus (−) conjugate nuclei, at the time of each division, thus giving dimorphic expressions in cells and parts of cells comparable to the general development of sexual dimorphism in gametangia and the vegetative tissues beyond the gametangia. In this sense clamp connections can be compared directly with the hook-shaped structures in the Ascomycetæ. They do not necessarily imply any close derivation of the Basidiomycetæ from the Ascomycetæ, althought there can be no question but that Ascomycetæ and Basidiomycetæ are a monophyletic group of two more or less parallel series and that these in turn constitute a monophyletic group together with the Phycomycetæ, but not derived directly from them.

The orthogenetic evolutionary movement shown in the point of determination of the incomplete primary sexual states duplicates in a remarkable manner similar orthogenetic evolutionary movements in the time of secondary sex determination in the groups of sexual algæ, in the gametophytes of the Metathallophyta, and in the sporophytes of the heterosporous plants. In each of these series the evolution continues in a progression through the ontogeny of the individual, from determination at the end of the ontogeny to determination at the very beginning of the ontogeny when the extreme forms are reached. Such processes and relationships must be fully understood before correct phyletic taxonomies can be established.